Habitat ecology of three different species of whirligig beetles (*Gyrinidae*) in the East Usambara Mountains, Tanzania

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Abstract

An animal's requirements towards its habitat are described by the niche concept. A fundamental principle of this concept is that it is not possible for two species to coexist in the same niche. In this study factors influencing niche differentiation among three species of whirligig-beetles of the family *Gyrinidae* (*Dineutes sp, Orectochilus sp, Gyrinus sp*) were investigated. To compare preferences of habitat cover and current speed and to investigate competition, in situ measurements and experiments were conducted. *Orectochilus sp* was more abundant in shaded habitats, whereas *Dineutes sp* and *Gyrinus sp* were more abundant in open areas. Experimental measurements did confirm these findings for *Gyrinus sp* and *Orectochilus sp*. There was no significant difference among the three species abundances in relation to current speed, though comparing *Dineutes sp* and *Gyrinus sp* showed preference of *Dineutes sp* for slow flowing, almost standing water bodies. Experiments investigating current tolerance showed differences between species but they were not correspondent to the conclusions drawn from the field study. Clear evidence for interspecific competition could not be shown. Based on these results it can be concluded that habitat cover has an influence on niche differentiation in *Gyrinidae* species whereas current speed and interspecific competition could not be identified as major factors. Other abiotic and biotic factors are most likely to play a more important role.

Introduction

The needs of an organism are defined in the concept of the ecological niche. Hutchinson (1957) describes a species niche as an n-dimensional hypervolume within which a species can theoretically maintain a viable population. The dimensions include physical, chemical and biological parameters. This “fundamental niche” can be limited further by biotic interactions like competition for resources with other species or by predation resulting in the “realized niche” (Hutchinson 1957) which is the hyperspace within which the organism actually lives. It is not possible for two different species to coexist in exactly the same niche. Thus, coexistence of species goes along with niche differentiation, a principle referred to as the competitive exclusion or Gause’s principle (Begon et al. 1990). This niche separation can be established through habitat selection, temporal differences in activity, diet or character displacement (Price 1984). Differences are accentuated in zones of overlap and weakened in parts of the range outside this zone (Brown & Wilson 1956).

The aim of this study was to investigate abiotic and biotic factors affecting the habitat selection of three different species of whirligig beetles (*Gyrinidae*) and to analyse factors of niche differentiation and possible interspecific competition.

The following questions were asked:

1) Do the three studied species differ in their preference for abiotic factors like habitat shading and the amount of sunlight exposure?
2) Is there a difference in current tolerance between the species which leads to different species abundances in differentially flowing water?
3) Is there interspecific competition between the species over resources such as space and food and do the species differ in their competitive ability?

Study species

The *Gyrinidae* comprises about 700 described species in 11 genera. They are aquatic, elliptical shaped adephagan beetles with short antennae and completely divided eyes (Booth et al. 1990). They are surface scavengers in usually gently flowing freshwater systems. Their main food consists of insects that have fallen onto the water. With their divided eyes they are at the same time able to look out for enemies within and above the water. On being alarmed they move rapidly and show a characteristic “whirling” in circular patterns, which gave them their common name “whirligig beetles”. *Gyrinidae* are excellent divers and able to fly well in order to disperse. Their complete lifecycle is water-dependent, the larvae usually dwelling on the bottom of pools and slow flowing streams (Skaife 1979).

In a study area around the Amani Nature Reserve, East Usambara, Tanzania, three different species of *Gyrinidae* were found and could be identified to genus and morpho - species. These species differ significantly in size and also in colour patterns. *Dineutes sp* is the biggest species with a rounded body and dark ventral side; *Orectochilus sp* is the medium-sized species with an elongated, stream-lined body, long abdominal appendix and a bright yellow ventral side and *Gyrinus sp* is the smallest species, about half the size of the medium one and with a slightly more orange ventral side.

Study area

This study was conducted at Amani Nature Reserve in the East Usambara Mountains (4º 48’, 5º 13’ S; 38º 32’, 38º 48’), Tanzania, a region of about 1.300 km² covered with submontane tropical rain forest, cleared farmland, tea estates and plantations (Hamilton 1989). Sampling took place at four different sites around the village of Amani and included a fast-flowing erosive stream with pools of lower current in it (erosive river), a floodplain (floodplain), a mostly standing water body (Amani pond) and a river with both fast and gently flowing water (Emau river). All samples were taken during the late dry season in September 2003.

Materials and Methods

Abundance

In the four different river systems, a sampling area of about 100 m length was chosen (except for the Amani pond where a length of approximately 80 m was chosen owing to its smaller size). We divided this area into 25 (20) transects of 4 meters length and the number of *Gyrinidae* in 12 of these transects was estimated. The average abundance of each species within 4 m was calculated and extrapolated to the entire 100 m study site.

Measurements of the abiotic factors of the habitat

After recognition of a group or single individuals of one of the three species, four factors were measured: temperature, percentage of overhead forest cover, width of the habitat (river), and current speed. Temperature was measured with an Enviro-Safe thermometer (LaMotte, Model 545, Code 1066). For measuring cover we estimated the percentage of visible sky at each site (100% = open, 0% = totally shaded). The width of the river was measured with a measuring tape. To measure the current speed we timed the passage of a surface float. Where the beetles were found, a stick was thrown into the river and the time for passing 1 m was taken. With this the current speed was calculated in m/s.

For each river system we took as many samples for each of the three species of *Gyrinidae* as possible (maximally 15). The data for each species and factor were analysed using one-way Analyses of Variance (ANOVA) to compare between species.

Experiments

<u>Cover experiment</u>

Three trays (55 x 45 x 10 cm) were placed in a "quiet" corner of a laboratory veranda giving as much exposure to sunlight as possible without exposure to heavy rain. Every tray was divided into three different, equal areas (shade, semi-shade, open). Cover was created by bamboo frames on which leafs were laid. Five individuals of each species were put into one tray (= 3 treatments). To prevent the individuals from escaping we covered the trays with transparent plastic film. The position of the individuals in the trays was noted four times each day (9.00, 12.00, 15.00 and 18.00 local time) with four replicates per treatment. The number of individuals observed per area and species over all replicates was calculated and analysed with a Chi-square test.

<u>Current experiment</u>

To generate different current speeds one end of a split bamboo cane about 2.50 m length and about 6 cm diameter was placed in a waterfall of the erosive river so that water flowed along it. To regulate the speed we changed the angle of the bamboo cane. After generating a current speed and measuring it with the float method (mean of ten measurements), five individuals of each species were placed individually in the cane and the time for which they could resist the current (swimming time) was taken. If an individual resisted (remained in the cane without being washed out) for two minutes the experiment was stopped. The experiment was done using nine different current speeds.

Individuals that were washed away/escaped were replaced. The tolerance of each species towards current speed was analysed using a general linear model.

Behavioural experiments

To investigate the interspecific competition between the three species, three individuals of two or three species respectively were placed together in different aquaria covered with plastic film (see Table 1). The aquaria were placed on a quiet veranda. For one day every hour (14.00 – 23.00) the spatial distribution, the movements and other interactions between the species were noted using a combination of scans and five minutes of observation.

Table 1. Experimental arrangements for testing possible competition between individuals of three species of *Gyrinidae* (Coleoptera).

Aquarium	Species
1	*Dineutes sp* + *Gyrinus sp*
2	*Dineutes sp* + *Orectochilus sp*
3	*Orectochilus sp* + *Gyrinus sp*
4	*Dineutes sp* + *Orectochilus sp* + *Gyrinus sp*

Feeding experiments

Feeding experiments were conducted to investigate further interspecific competition for resources. The same combinations as in the behavioural experiments were used. At two-minute intervals insects were dropped into the aquarium (six repeats) and the species that seized the prey was noted. Additional notes were made about aggression within and between species. The experiment was carried out three times a day (9.00am, 14.00pm, 18.00pm) over two days using different prey sizes (fruit flies: *Drosophila sp*, ants:

Formicinae). Feeding success rates for each species were compared with a nonparametrical sign-test (Zar 1984).

Results

Abundance

The average abundance of the three species of *Gyrinidae* per 4m length in the four different habitats is shown in Table 2. In Amani Pond all three species were found together; in Emau River only *Dineutes sp* and *Orectochilus sp* were present; in the floodplain there were *Orectochilus sp* and *Gyrinus sp* and in the erosive river only *Orectochilus sp.* could be found.

Table 2. Average abundance of three species of *Gyrinidae* in four different habitats close to Amani, Tanzania. The abundance (± S.D.) within an area of 4 m length is shown.

Species	Emau River	Amani Pond	Floodplain	Erosive River
Dineutes sp	0.50 (± 1.17)	7.17 (±17.55)	0.00	0.00
Orectochilus sp	1.00 (± 1.48)	0.50 (±1.22)	15.00 (±22.18)	3.58 (± 5.84)
Gyrinus sp	0.00	0.50 (± 1.22)	7.58 (±11.25)	0.00

Habitat measurements

Abundance of the three species was compared with habitat cover, current speed and the width of the water body (Table 3).

Table 3. Analysis of variance p-values (significance level 0.05) for different habitat factors selected to occurrence of three species of *Gyrinidae* in locations close to Amani, Tanzania.

Habitat factor	p - values
Current speed	0.338 (n.s.)
Cover	< 0.001 (significant)
Width of water body	0.143 (n.s.)

A significant difference in abundance in response to cover was found. *Orectochilus sp* was more abundant in shaded areas than *Dineutes sp* and *Gyrinus sp* Figure 1 shows the variance in distribution among the three species of *Gyrinidae* with 25 – 75 % of the variation plotted in the boxes and total range indicated by solid lines. Within each box the median is given by a horizontal line. Means are indicated by solid diamonds. For *Gyrinus sp* all animals were found in the open (100 %), except for two outliers (asterisks). Additionally species pairs were compared (Table 4).

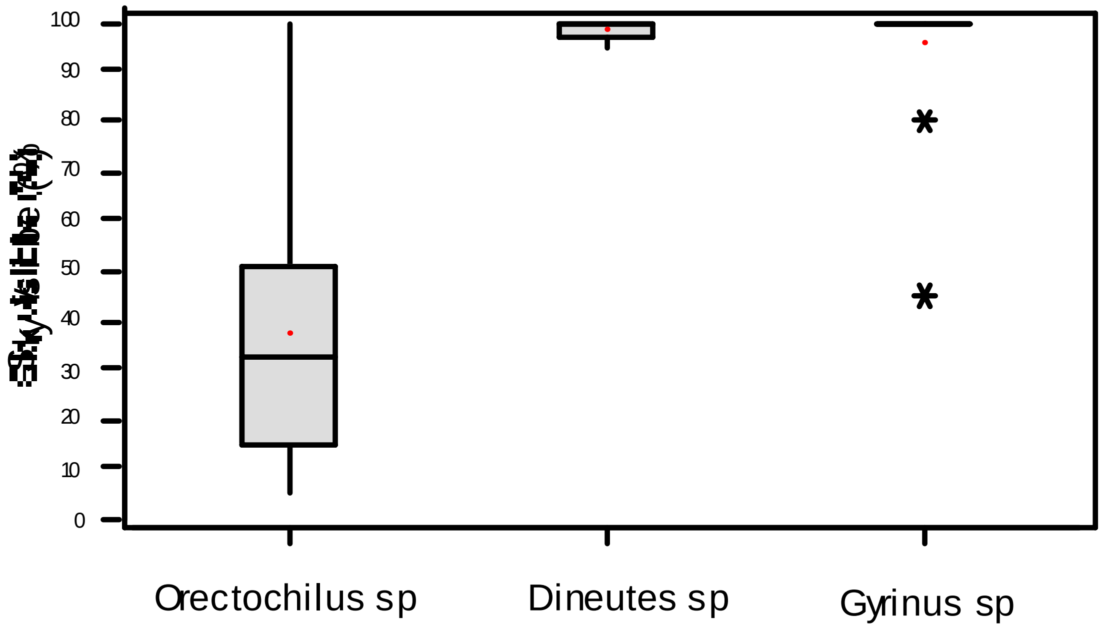


Figure 1. Abundance of three Gyrinidae species in differently covered habitats close to Amani, Tanzania

Table 4. Analysis of variance (p-values) between species-pairs for different habitat factors at locations near Amani, Tanzania.

Habitat factor	***Dineutes sp* vs. *Gyrinus sp***	***Orectochilus sp* vs. *Dineutes sp***	***Orectochilus sp* vs. *Gyrinus sp***
Current speed	0.006 (significant)	0.252 (n.s.)	0.643 (n.s.)
Cover	0.511 (n.s.)	< 0.001 (significant)	< 0.001 (significant)
Width	0.04 (significant)	0.95 (n.s.)	0.062 (n.s.)

The only significant difference between *Orectochilus sp* and the other two species was found in habitat coverage. Between *Gyrinus sp* and *Dineutes sp*. there was no difference in abundance based on habitat cover but they differed in regards to current speed and width of the habitat. *Dineutes sp* was more abundant in slower flowing (Figure 2), larger water-bodies.

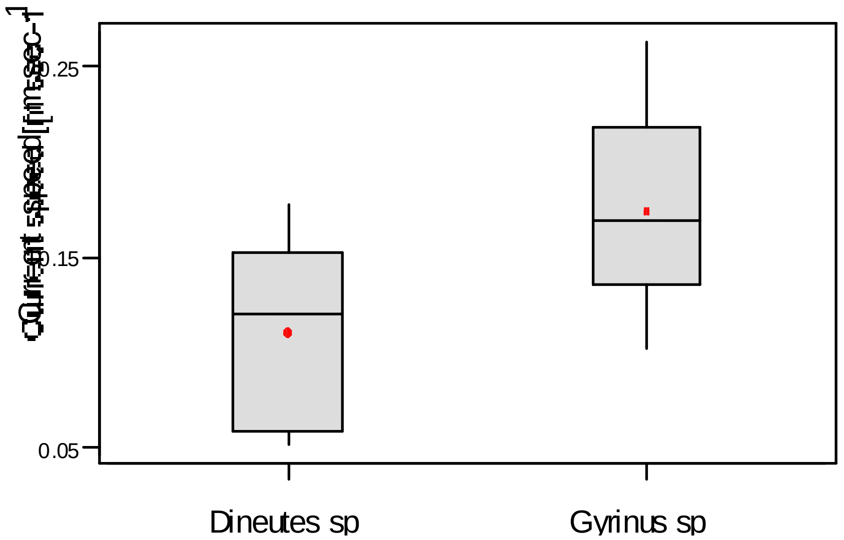


Figure 2. Abundance of the *Gyrinidae* species *Gyrinus sp* and *Dineutes sp* in different current speeds in habitats close to Amani, Tanzania

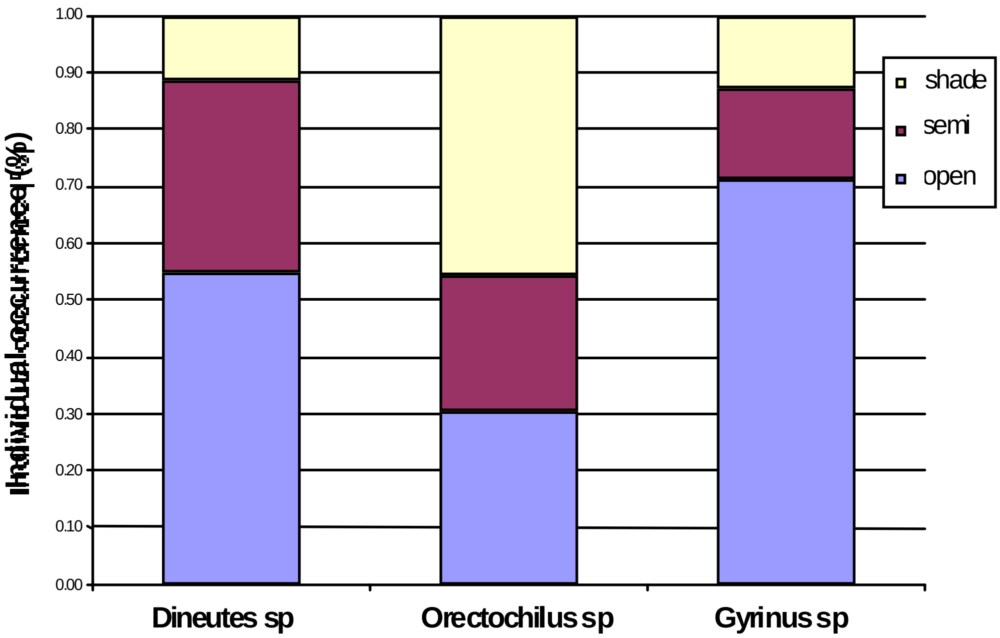
Experiments

Cover experiment

There was a significant relationship between species and differently covered areas in the trays (p < 0.001, df = 4). *Orectochilus sp* tended to be more in the shade (30 observed individuals compared with 14.67 expected by chi-square test; n = 66) while *Gyrinus sp* preferred open areas (50 compared with 36.94; n = 70). For *Dineutes sp* no real preference for a particular condition could be shown (open: 44 compared with 42.22, shade: 9 compared with 17.78; n = 80). Figure 3 shows the “cover preference” for all three species according to the percentage of counted individuals in particular areas (open, semi-shade, shade).

Current experiment

The general linear model showed a strong correlation between current speed and the time the beetles can resist it (swimming time, $p < 0.001$). The stronger the current, the sooner the beetles were washed away. For slow-flowing water no significant difference could be found between species ($p = 0.255$), but there was a significant interaction between current and species ($p = 0.04$), showing that the *Gyrinidae* differ in their ability



to withstand current (Figure 4).

Figure 3. Cover - preference of three species of *Gyrinidae* according to the percentage of counted individuals during a cover experiment.

Behavioural & feeding experiment

No statistical analysis was done on the behavioural data. Looking at the spatial distribution of the different species in the aquaria a tendency to avoid the other species introduced rather than to mix with it seems likely. No territorial behaviour, or a separation into different areas of the aquarium was observed. *Dineutes sp* seemed to aggregate more than the two others, a tendency that was also noticed during data collection in the field. Movement and agility seemed to slow down towards the evening with many beetles even leaving the water (sitting on stones, the wall etc.). In the three-species-treatment, only *Dineutes sp* was found in the water, the others sitting on the walls and stones. Two out of the three *Gyrinus sp* died during the experiment. Generally very few interspecific contacts were observed. The feeding experiments were only carried out with fruit flies as the beetles did not take the offered ants. Except for the *Orectochilus sp - Dineutes sp* treatment there were no significant differences in foraging success between the species (Table 5).

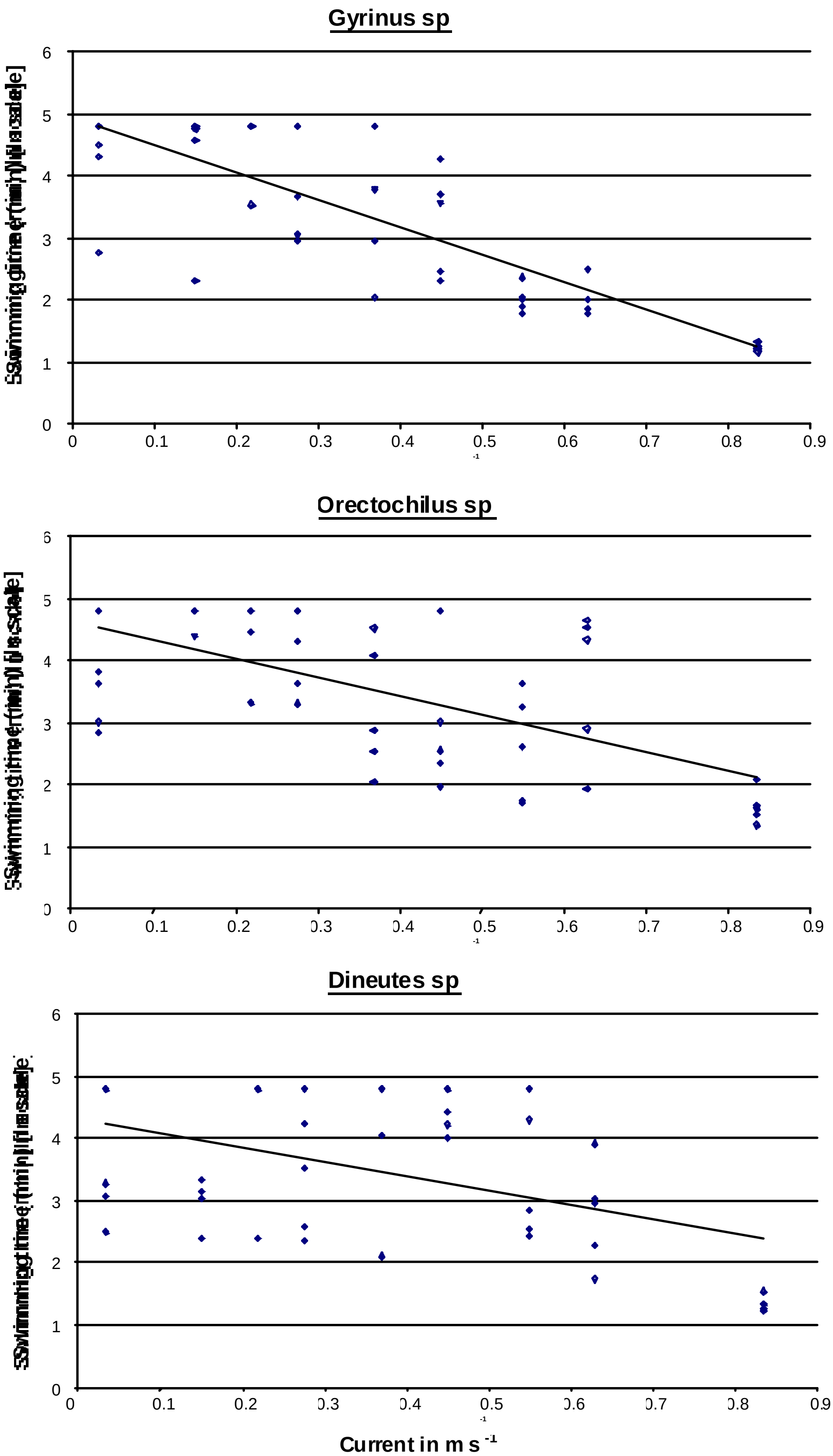


Figure 4. Current tolerance as a function of swimming time (ln transformed) in experimental studies of three different species of *Gyrinidae*.

Table 5. Number of insects eaten per unit time by different species of *Gyrinidae* in three different experimental treatments.

Treatment	*Dineutes sp*	*Orectochilus sp*	*Gyrinus sp*	p
Dineutes sp. - Orectochilus sp.	5	12	*	0.04721
Dineutes sp. - Gyrinus sp.	8	*	2	0.10938
Orectochilus sp. - Gyrinus sp.	*	11	6	0.22559

Orectochilus sp was more successful than *Dineutes sp* in collecting insects (p = 0.047). In the three-species-treatment only *Dineutes sp* took food on five out of 12 occasions. The three individuals of *Gyrinus sp* in this treatment all died and were probably eaten (though this was not observed), as did two individuals of *Orectochilus sp*.

The only obvious interspecific aggressive behaviour was observed in the three-species treatment where *Dineutes sp* was seen chasing the other two species.

Discussion

According to the competitive exclusion principle it is not possible for two different species with the same niche requirements to form steady-state populations in the same region (Hutchinson & Deevey 1949). In order to allow coexistence there must be some form of niche separation. The aim of this study was to gain some insight into the modifications and ecological factors that allow three different species of the family *Gyrinidae* to coexist in the freshwater systems of the East Usambara Mountains. This task was approached with a combination of field studies and experimental designs to test for different abiotic and biotic factors. Three major aspects of the beetles' environment were investigated: the amount of coverage of the habitat by canopy trees, the current speed of the water and competition between species. Additionally measurements of the width of the water bodies were taken.

Influence of habitat coverage

The results from the habitat measurements in the field show that *Orectochilus sp* is found significantly more often ($p < 0.001$) in shaded habitats than the two other species, which are most abundant in open areas with little or no cover by vegetation

(Figure 1). For *Dineutes sp* and *Gyrinus sp* no difference in their preferences for sunlight exposure could be shown. To further investigate these findings, an experiment was done which looked at the cover preference of the beetles (Figure 3). The results support the conclusions drawn from the field study by showing that *Orectochilus sp* prefers shaded areas, whereas *Gyrinus sp* is found in open areas. *Dineutes sp* showed no clear preference for open areas, a result which is opposed to the conclusions from the habitat measurements. Therefore it seems likely that the greater abundance of *Dineutes sp* in open areas is due to other factors and not to a limitation through a low tolerance towards shade.

Influence of current speed

Comparison of the abundances of all three species to current speed showed no significant result (Table 3). There was no difference between the three species based on the flow of the water. Nevertheless *Dineutes sp* and *Gyrinus sp* do differ ($p = 0.006$), as *Dineutes sp* is more abundant in standing or very slow flowing water (Figure 2).

The experiment in current tolerance was conducted to test the current speed tolerance of the species. Its results show an interaction between species and current speed but not as expected from the habitat measurements. In their natural habitat *Dineutes sp* occur only in very slow flowing almost standing water bodies, while in the current-experiment they turned out to be the most resistant against strong current (Figure 4). *Gyrinus sp*, which was found in similar currents as *Orectochilus sp* on the other hand, was least tolerant. There are differences in the tolerance of the three species towards current but they do not explain the distribution pattern found in the field. From this study no supporting evidence for a niche separation based on current speed can be drawn.

Influence of habitat width

The comparison of the width of the habitats among all three species did not show a significant difference. There was a significant difference ($p = 0.04$) between *Dineutes sp* and *Gyrinus sp* if just those two are compared. *Dineutes sp* seems to prefer larger areas than *Gyrinus sp*, but the importance of this finding as a limiting factor has not been further investigated.

Influence of interspecific competition

In the field mixed populations of two of the three *Gyrinidae* species were occasionally found but never the combination *Dineutes sp* with *Orectochilus sp* or a population of all three species. This might imply some form of interspecific competition. Competition is known to have a major influence on a species' actual or realised niche (Price 1984) and therefore two experiments were conducted to gain some insight into possible competition for resources between the *Gyrinidae* species.

In the behavioural observations, spatial distribution in four differently combined populations was analysed and a tendency to avoid interactions between species seems likely as there were few observed interactions. However results were not clear enough to say that there is competition avoidance going on, especially because no hint of a division of the experimental habitat between the species could be found. Striking is the three-species-treatment aggression levels were high and the beetles were more often seen out of the water than in the other treatments. Only *Dineutes sp* was observed in the water and aggression of this species towards the others was noted on several occasions. The fact that all *Gyrinus sp* died, might be a hint that under high levels of competition, it has the least ability to resist.

Interestingly no higher level of competition became obvious in the *Dineutes sp – Orectochilus sp* treatment, which leaves the question unanswered why this combination does not seem to occur in the field.

The feeding experiments showed no clear advantage of one species over the others in terms of foraging success. In the *Dineutes sp - Orectochilus sp* treatment *Orectochilus sp* had a significantly higher feeding-success rate than *Dineutes sp* ($p = 0.04721$), which might be due to the greater agility of the first. As this is the only species combination not found in any of the study sites we might suggest that *Orectochilus sp* is able to displace *Dineutes sp*. This competition for food resources might be one reason for the differences between *Dineutes sp*'s realised and fundamental niche.

In the three-species-treatment, the dead *Gyrinus sp* and *Orectochilus sp* were eaten and an active killing of these beetles by others cannot be excluded, though it was not observed.

Considering these findings, it can generally be said that the three studied *Gyrinidae* species differ in their niche requirements as it is proposed by Gause's principle (Hutchinson& Deevey 1949; Price 1984). The exposure of the habitat to sunshine is likely to be a factor affecting habitat selection. Both measurements in the natural habitat and experiments showed a preference of *Orectochilus sp* for shaded habitats while *Gyrinus sp* prefers open areas. *Dineutes sp* showed much greater tolerance towards different coverage and also towards current speed as expected from its natural distribution.

An influence of current speed on the distribution of the three species could not be found, even though the species show different tolerance towards strong current. The difference in resistance might be due to differently shaped bodies, favouring the bigger, stronger *Dineutes sp* and the highly streamlined *Orectochilus sp* over *Gyrinus sp*.

No clear conclusions can be drawn from the behavioural and feeding experiments, competition avoidance seems likely although it remains unanswered how much the species actually compete for the same resources.

In order to gain more specific insight into the role of current and interspecific. Competition on the niche shape of these *Gyrinidae* species, further studies are necessary. The current experiments seem to be an effective way to test tolerance but there were also some major disadvantages involved. Current flow was not consistent over the whole length of the test arena and beetles often had the possibility to resist the current by climbing on the walls or diving. There were also quite a lot of individuals that escaped which might have had some influence on the data as they had to be replaced. Further standardisation of the method is advisable. In order to see species differences in low current it is necessary to increase the time limit for each experiment since 120 seconds were probably too short to show differences in resistance ability.

The behavioural and feeding experiments showed few useful results mostly due to a lack of time in order to do more replicates. More sophisticated experiments and longer observational sessions in situ and in the lab might shed some light on the role and amount of competition among the different species.

Finally and probably most importantly more ecological factors such as competition with other species occurring in the same habitat and the rate of food supply (insects dropping onto the water surface) should be included in the study to get a greater insight and a more complete picture of the different niches.

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